

Electronic Supplementary Materials to:

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Table of contents

Appendix 1. Historical records of right whales and gray whales in the North Atlantic.....	2
North Atlantic right whale	2
Gray whale.....	5
Appendix 2. Historical and archaeological context, molecular analyses and dating of the analysed specimens	8
Historical and archaeological context of specimens	8
Collagen PMF and Ancient DNA Barcoding	11
Dating	13
Appendix 3. Historical accounts mentioned in the main text	15
Supplementary references	20

Appendix 1. Historical records of right whales and gray whales in the North Atlantic

North Atlantic right whale

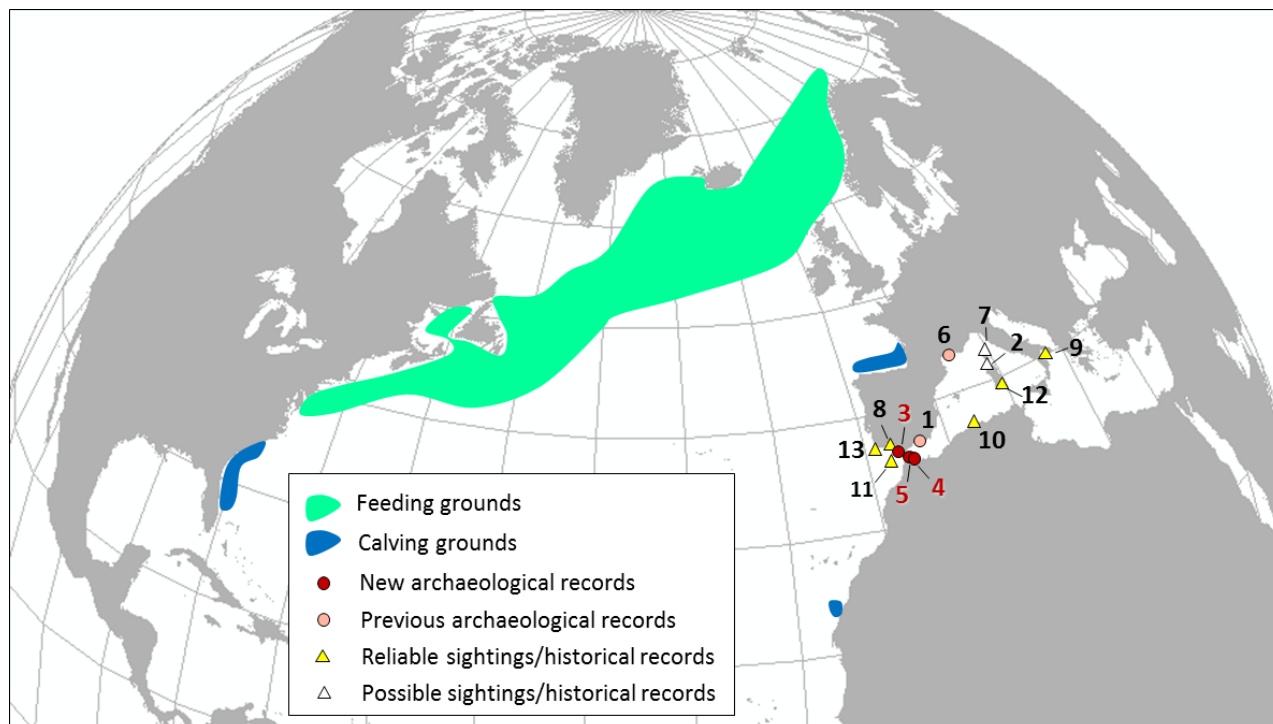


Figure S1. Summary of current knowledge on the historical distribution of the North Atlantic right whale (*Eubalaena glacialis*), with a focus on records in the Mediterranean Sea and nearby Gibraltar area. Estimated distribution of summer feeding grounds is adapted from [1]. Calving grounds in the western North Atlantic correspond to current grounds, based on recent sightings [2]. The winter calving grounds in the Bay of Biscay and northern Spain are known from Basque and Spanish whaling records [3,4], whereas the small calving ground in Cintra Bay, Western Sahara, is known from American whaling records [5]. Symbols and numbers refer to records in the Mediterranean Sea and Gibraltar area (detailed in table S1), including six reliable sightings or historical records of live individuals (yellow triangles), two possible historical records (white triangles), two previous archaeological records (light red circles), and three archaeological records added by the present study (dark red circles).

Table S1. Review of known and inferred North Atlantic right whale records in the Mediterranean Sea and Atlantic area adjacent to the Strait of Gibraltar. Map reference numbers are those in figure S1; laboratory references as in Table 1. Date: str –from stratigraphy; cal¹⁴C – from radiocarbon analyses. For records 3, 4 and 5 (added by the present study) see table 1 and figure 2 for more details.

Map ref. (lab. ref.)	Date	Location	Details
1 ●	Upper Magdalenian str: ca. 14,000 BP	Málaga, southern Spain	167 plates of two whale barnacle species (<i>Tubicinella major</i> , <i>Cetopirus complanatus</i>), in Narja Cave, in an Upper Magdalenian archaeological context [6]. Whale barnacles are obligate commensals of whales, and these two species are only known to associate with right whales (<i>Eubalaena</i> sp.) [7], so this is indirect evidence of right whale presence. This record corresponds to a period (during the last glaciation) when the climate was very different from today's.
2 △	3 rd Century	Near the strait between Corsica and Sardinia	Aelian described “ram-fishes”, sea-monsters with a “white band running round its forehead [...] as the tiara [of a] King of Macedon”, which spent winter “near the strait between Corsica and Sardinia”. These may correspond to right whales [8] (see discussion in Appendix 3).
3 ● (WH812)	Late Antiquity cal ¹⁴ C: 232BC – 23 BC	Tarifa, Cadiz, Spain	A vertebra found in the <i>Baelo Claudia</i> archaeological site (excavations by M. Ponsich in the 1980s; said to come from the filling of the Vat at Conjunto Industrial VI). Later analyses [9] include dating through cal ¹⁴ C (with the Marine9 calibration curve). It has a series of cut marks on its flat surface, possibly indicative of having been used as a fish-cutting table [9,10]. This study: species identified through ancient DNA barcoding as <i>Eubalaena glacialis</i> , and through collagen PMF analysis as Balaenidae.
4 ● (WH822)	Late Roman str: 320 AD – 425 AD cal ¹⁴ C: 180 AD – 396 AD	Tetouan, Morocco	A rib (cut and worked) found in the <i>Tamuda</i> archaeological site (excavations by M. Tarradell in 1955; specimen subsequently kept in the Tetuán Museum). Later analyses [11] inferred date from analysis of the archaeological context (pottery and coins in the same layer when studying the materials in the museum), dating through cal ¹⁴ C (with the Marine13 calibration curve), and interpretation of the object as a carpenter's tool. This study: species identified through ancient DNA barcoding as <i>Eubalaena glacialis</i> , and through collagen PMF analysis as Balaenidae.
5 ● (WH818)	Late Roman str: 475 AD – 500 AD cal ¹⁴ C: 226 AD – 410 AD	Ceuta, Spain (N. Africa)	A rib fragment (burned), found in the <i>Septem</i> archaeological site (Plaza de África 3 dig, UE 4018) in 2006 [12]. This study: species identified through collagen PMF as Balaenidae, very likely <i>Eubalaena glacialis</i> ; dating through cal ¹⁴ C (IntCal13 calibration curve, + 400 years to correct for the marine reservoir effect).
6 ●	Late Antiquity	Gruissan, Aude, Southern France	A whale vertebra, found in the Saint Martin Island archaeological site in Gruissan [13]. Identified through ancient DNA barcoding and collagen PMF as <i>Eubalaena glacialis</i> [14].
7 △	1620	Corsica, France	Lacepède [15] mentioned a right whale (“ <i>baleine franche</i> ”) taken in Corsica in 1620, but provided no other details. This record is therefore very uncertain, corresponding to an event 200 years before, when whale taxonomy was still poorly established.
8 ▲	1808	Cadiz, Spain	Graells [16] cited the 1817 work “ <i>Peces del Mar de Andalucía</i> ” by Antonio Cabrera, in which there is a reference to a whale identified as “ <i>Balaena Mysticetus</i> ” that stranded dead in 1808 in the Cadiz beach. The description is consistent with a right whale: an enormous head, occupying a third of its body (which was 20 “ <i>varas</i> ” long, about 16 m) had a huge mouth, a black back and white belly.

9 ▲	1877 (9 Feb.)	Gulf of Taranto, Italy	A right whale was captured in the Taranto beach, and painted from life in watercolour by Alejandro Hueber (reproduced in [16]). The realistic representation leaves no doubt about the species. The depiction of head callosities indicates that it was an adult.
10 ▲	1888 (20 Jan)	Algeria	Two right whales were seen in the waters off Alger, between Castiglione (Bou Ismail) and Tipaza (Algeria). One got entangled in the tuna traps and stranded on the sand, being captured by fishermen. It measured about 11 m of length and 6.6 m of girth (indicating that it was an adult). The skeleton was recovered by the Paris Museum [17], leaving no doubt about its identification.
11 ▲	1921 (May, or April?)	Strait of Gibraltar region	Known from the report of a technical visit (by Rodríguez Santamaría, cited by [18]) to the Getares factory (in Algeciras), which was supplied by whaling boats operated by Norwegian whalers. Rodríguez Santamaría mentions baleen plates of 2 m, which can only have come from (one or more) adult right whales. The exact location where these were captured is not known, thus location in figures 1 and S1 is very approximate.
12 ▲	1991 (May)	Sardinia, Italy	Sighting of an individual right whale reported by Rossi (1996, cited by [19] and [20]).
13 ▲	1994 (3 Feb)	Cape St, Vicent, Portugal	Detailed report of the sighting of an adult and calf off Cape St Vicent (37°07'N, 08°58'W) [21]. Calf estimated to be very young (2 months) based on size in relation to adult.

Gray whale

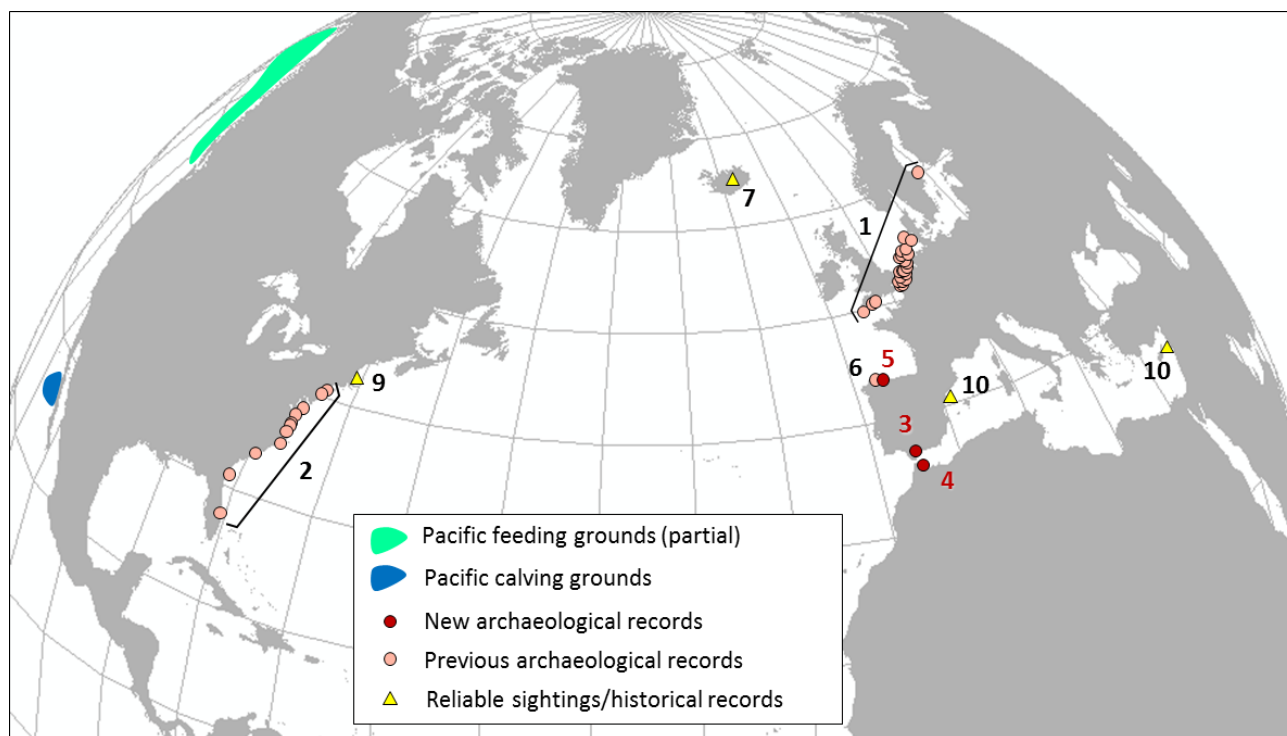




Figure S2. Summary of current knowledge on the historical distribution of the Atlantic population of gray whale (*Eschrichtius robustus*), with a focus on records in the Mediterranean and northern Iberia. Current winter calving grounds and (part of) the summer feeding grounds in the Pacific are illustrated for reference [22]. Symbols and numbers refer to records in the North Atlantic and Mediterranean Sea (detailed in table S2), including historical records or recent sightings (yellow triangles), previous archaeological records (light red circles), and three archaeological records added by the present study (dark red circles, red numbers 3-5).

Table S2. Review of known gray whale records in the North Atlantic and Mediterranean Sea. Map reference numbers are those in figure S2; laboratory references as in table 1. Date: str –from stratigraphy; cal¹⁴C – from radiocarbon analyses. For records 3, 4 and 5 (added by the present study) see table 1 and figure 2 for more details.

Map ref. (lab. ref)	Date	Location	Details
1 ●	cal ¹⁴ C: > 50 k BP to late 17 th century	Western Europe	Over 30 bone specimens have been identified as gray whale in Western Europe, the southernmost ones in Cornwall, UK [23,24], the northernmost ones in Graso, Sweden [25], and mostly concentrated in the southern North Sea [26]. Those which have been dated range from over 50,000 years old to the late 17 th century [26–28].
2 ●	cal ¹⁴ C: 48 k BP to late 17 th century	USA Atlantic coast	At least 12 bone specimens have been identified as gray whale in the Atlantic coast of the United States, ranging from the southeast coast of Florida [29] to Long Island in New York State [27,29,30]. Those with known dates range from ca. 48,000 BP to the late 17 th century [27,30]. The southernmost records, from Florida [29] and Georgia [30] correspond to immature individuals, supporting the hypothesis that Atlantic gray whales previously calved in this region.
3 ● (WH815)	Late Roman str: 475 AD - 525 AD cal ¹⁴ C: 251 AD - 422 AD	Algeciras, Spain	A half vertebra found in the <i>Iulia Traducta</i> archaeological site in 2001 (San Nicolas 3-4 Fish salting plant, UE 1416) [9]. This study: species identification through collagen PMF as <i>Eschrichtius robustus</i> ; dating through cal ¹⁴ C (IntCal13 calibration curve, + 400 years to correct for the marine reservoir effect).
4 ● (WH820/ WH821)	Late Roman str: 400 AD - 450 AD cal ¹⁴ C: 71 AD – 245 AD	Tetouan, Morocco	One bone fragment (cut and worked) from the <i>Tamuda</i> archaeological site in 2012 (unpublished abandonment of the Eastern <i>Balneum</i> – sounding 8, UE 864) [31]. This study: species identification through collagen PMF and ancient DNA barcoding as <i>Eschrichtius robustus</i> ; dating through cal ¹⁴ C (IntCal13 calibration curve, + 400 years to correct for the marine reservoir effect).
5 ● (WH810)	Pre-Roman str: 400 BC – 200 BC	Gijón, Asturias, Northern Spain	Whole scapula (with cut marks) found in La Campa de Torres archaeological site in 1996, and identified using anatomical methods as gray whale, <i>Eschrichtius robustus</i> [32]. This study: confirmation of the species' identification through collagen PMF.
6 ●	13th-18th Centuries	Cudillero, Asturias, Northern Spain	Mandible, sampled underwater in 2014, in the Medieval whaling port of Luanco. Dating corresponds to the centuries when the whaling port was active. Identified through ancient DNA barcoding as <i>Eschrichtius robustus</i> [33].
7 ▲	1230 - 1706	Iceland	Multiple Icelandic natural history studies list (and sometime illustrate) whale species, including one " <i>sandlægja</i> " ("sand-lier") or " <i>sandæta</i> " ("sand-eater"), whose behaviour and physical characteristics match the gray whale. These studies have been reviewed and analysed by Lindquist [34] who concluded that, taken together, they indicate that gray whales were well-known (including accurate detail on behaviour and ecology), killed (by spearing and lancing in shallow waters) and eaten. He also concluded that the species must still have been regularly seen and captured in Iceland up to 1700, but must have started to disappear soon afterwards.
8 (not mapped)	Before 1611	Unknown	A list of eight " <i>sorts of whales</i> " indicating " <i>the differences of goodnesse between the one and the other</i> ", provided to Thomas Edge in 1611 as part of his commission by the Muscovy Company for starting a whaling operation in Spitzbergen (Svalbard) [35]. Sorted by decreasing order of commercial interest, in fourth position (after the bowhead, right and sperm whales) is the " <i>Otta Sotta</i> ", whose description matches the gray whale, and that " <i>yields the best Oyle</i> " (see [27,36] for further discussion). There is no location for this record: the list was done ahead of whaling in Spitzbergen (and hence it is not a list of whales found in Spitzbergen); it comes almost certainly from Basque sources, but at the time Basques whaled across the North Atlantic [37].

9 	1725	New England	In his <i>"Essay upon de Natural History of Whales"</i> , Dudley lists the sorts of whales found on the coast of New England [38]. The second of this (after the right whale), is the <i>"Scrag Whale"</i> , whose description matches the gray whale. He also mentions that this species <i>"is nearest the right Whale in Figure and for Quantity of Oil"</i> , thus commercially interesting, even if not having valuable baleen (<i>"his Bone [...] won't split"</i>).
10 	2010 (May)	Israel and Barcelona	A single gray whale sighted off the Israeli Mediterranean shore; then same individual being seen again off Barcelona 22 days later (supported by photographic evidence) [39]. Given the total absence of known records of gray whales in the North Atlantic for more than two centuries, this individual was most likely a vagrant from the Pacific population [39].

Appendix 2. Historical and archaeological context, molecular analyses and dating of the analysed specimens

Historical and archaeological context of specimens

Table S3. Archaeological contexts and radiocarbon dating for the specimens analysed in the present study.

Lab Code	Specimen details	Excavation location	Excavation date	Conventional radiocarbon age	Calibrated radiocarbon age (Marine13)
WH810	Gray whale (scapula, whole bone with cut marks)	<i>La Campa de Torres</i> archaeological site, Gijón, Asturias, Spain [32]	1996	-	
WH812	North Atlantic right whale (vertebra, whole bone, with cut marks)	<i>Baelo Claudia</i> archaeological site (said to come from the filling of the Vat at Conjunto Industrial VI), Tarifa, Cadiz, Spain [40]	1980s	2440 +/- 30 BP [40]	232 BC – 23 BC
WH813	Fin whale (5 bone fragments)	<i>Baelo Claudia</i> archaeological site (Decumanus Maximus, unpublished excavation; Sounding 2, UE 214), Tarifa, Cadiz province, Spain (unpublished).	2009	-	
WH814	Long-finned pilot whale (vertebra, whole bone)	<i>Baelo Claudia</i> archaeological site (Maritime Baths, H-2, UE 2609), Tarifa, Cadiz province, Spain [41].	2013	1695 +/- 30 BP	642 AD – 773 AD
WH815	Gray whale (vertebra, half)	<i>Iulia Traducta</i> archaeological site (San Nicolas 3-4 Fish salting plant, UE 1416), Algeciras, Cadiz province, Spain [9]	2001	2045 +/- 30 BP	251 AD – 422 AD
WH816	Dolphin (vertebra, nearly whole bone)	<i>Septem</i> archaeological site (Puerta Califal, H-001), Ceuta (N. Africa), Spain [42]	2008	1580 +/- 30 BP	720 AD – 896 AD
WH817	Sperm whale (vertebrae or ribs, 5 inner bone fragments)	<i>Septem</i> archaeological site (Plaza de África 3 excavation, UE. 4042), Ceuta (N. Africa), Spain [43]	2006	2165 +/- 35 BP	88 AD – 296 AD
WH818	Likely North Atlantic right whale (rib fragment, burned)	<i>Septem</i> archaeological site (Plaza de África 3 excavation, UE 4018), Ceuta (N. Africa), Spain [12]	2006	2065 +/- 30 BP	226 AD – 410 AD
WH819	Likely African elephant (5 inner bone fragments)	<i>Tamuda</i> archaeological site (Sounding 7, UE 712), Tetouan, Morocco [44]	2010	-	
WH820 / WH821	Gray whale (one bone fragment, cut and worked)	<i>Tamuda</i> archaeological site (Sounding 8, UE 864), Tetouan, Morocco [31]	2012	2200 +/- 30 BP	71 AD – 245 AD
WH822	North Atlantic right whale (rib, cut and worked)	<i>Tamuda</i> archaeological site (excavations by M. Tarradell), Tetouan, Morocco [11]	1955	2085 +/- 35 BP [11]	180 AD – 396 AD

Gibraltar region

There is ample evidence of ancient well-developed fishery industries on both the European and the North African coasts of the western Mediterranean [45]. Their origins go back to the Phoenician-Punic period (at least 6th-5th centuries BC, probably earlier [46]), and were particularly well developed during the Roman period (from 206 BC in *Hispania Baetica*, southern Iberian Peninsula; and from 44 AD in *Mauritania Tingitana*, northern Africa). Archaeological work has revealed dozens of extensive industrial areas (*cetariae*), each with large vats, all located very near the shore [45,47] (figure S3). These were used for the production

of salted fish (particularly tuna) and fish-derived products such as fish sauces (e.g., *garum*), as corroborated by contemporary historical records (e.g. Strabo's *Geographica* Book III [45]). There is also evidence of trade through *amphorae* from the so called Circle of the Strait of Gibraltar to the entire expanse of the Roman Empire [48]. Most fish processing sites seem to have operated during the 1st and 2nd centuries AD, with a general decrease in the 3rd century and continuing till the late 5th or early 6th centuries AD [49,50].

Baelo Claudia (near today's Tarifa), in *Baetica*, was founded in the mid-2nd century BC, reaching its peak during the 1st and 2nd centuries AD, before declining at the end of the 2nd century and being abandoned by the 6th or early 7th century [51]. It was one of the largest Roman fish-processing sites in the southern coast of the Iberian Peninsula, and is the one in which more research has been conducted in the last decades (as the teaching field site for archaeology of the University of Cádiz [52]). Archaeological work shows evidence of fish processing from the 1st century BC, declining at the end of the 3rd century. Excavations have revealed two different areas used for fish processing: a smaller one and a much larger group of six complexes. A total of 8 *cetariae* have been excavated in Baelo Claudia, with a total estimated capacity of about 475 m³ [49,52]. Vaults are usually rectangular (the largest 2 x 3 m, 1.6 m depth) but also include four very large circular vaults (up to 3 m wide, 2.5 m deep; figure S3) that M. Ponsich suggested could have been used for processing whale meat [53,54]. Three bones presumed to be whales were recovered from *Baelo Claudia* (table 1): coming from ancient excavations at the site (WH 812), from mid-imperial layers from the *Decumanus Maximus* (WH 813), and from late-Roman from the abandonment vats at the Maritime Baths (WH 814) [55].



Figure S3. Fish processing plant (*cetaria*) in Baelo Claudia, with circular vaults (up to 3 metres wide). Photo by D. Bernal-Casasola.

Iulia Traducta, nowadays below the remains of modern “Villa Vieja” of Algeciras, in front of the rock of Gibraltar, was a Roman city founded just before the change of the era (Augustus times) and active until the Late Antiquity [56]. In the past decade, archaeological excavations have unearthed the industrial quarter of the city, dating most of the finds to the 5th century AD. Six *cetariae* are currently known, all of them in modern San Nicolás street. Specimen WH815 comes from “Conjunto Industrial I”, in 3-5, San Nicolas street. This is the largest and best preserved fish-salting plant, occupying more than 300 m² (17 x 19 m), and

including more than 30 vats of different dimensions, with total processing capacity of around 170 m³. It is one of the biggest salting-fish sites in the Gibraltar region, abandoned in the last moments of Late Antiquity [57].

Septem Fratres, in the southern coast of the Strait of Gibraltar, is located in the modern Spanish Autonomous City of Ceuta, with a strategic situation and an important harbour to control the commerce in the region [58,59]. From the 2nd century AD, and at least up to the late 5th century AD, it was dedicated to the exploitation of marine resources, as shown by five fish-salting plants in modern Gran Via street and surroundings. The three whale bone specimens we analysed (WH816, 817, 818) come from a rescue excavation conducted in 2006 at number 3, Plaza de Africa, where many mid and late-Roman halieutic dumps coming from the nearby *cetariae* were identified [60].

The *Tamuda* site is located in the Mediterranean coast of Northern Morocco, 7 km up the mouth of Martil river, in the Tetouan region, near the Rif Mountains. It's a Mauretanian (Hellenistic) city founded in the late 3rd or early 2nd centuries BC, in a site with previous Punic occupation. It survived until the mid-1st century AD when the Romans conquered the area, creating the *Mauretania Tingitana* province. From that time onwards, a military camp and *canabae* were installed in the central area of the archaeological site, which lasted till the first decades of the 5th century AD, when the Romans abandoned the area [61]. The site was inland but connected to the sea by the river, from where marine resources would have come, including from nearby fish-salting plants such as the one that existed in *Metrouna* (today's Sidi Abdeslam) in the early imperial times [62]. The three specimens analysed in this study were revealed by Moroccan-Spanish archaeological field work in the past decade: from recent excavations in the area of the northern mauretanian quarter (WH819; [63]) and from the eastern Roman *Balneum* (WH820, 821; [31]); and from a re-analysis of materials from ancient excavations stored in Tetouan Museum (WH822, a whale rib carved into a carpenter's plane; [11]). This work has also revealed a clay mould depicting a marine scene with a fisherman bearing a harpoon surrounded by marine animals interpreted as dolphins and possibly a whale [54].

La Campa de Torres, Asturias

The Archaeological site of La Campa de Torres is located in the Torres Cape, 7 km to the west of the city of Gijón (Asturias, Northern Spain), in the location of a pre-Roman fortified site built by the Astures people in the mid-7th century or early 6th century BC. Occupied by the Romans in the 1st century BC, it became the *Noega oppidum*, mentioned by multiple Roman sources as the location of a monument to the emperor Augustus. It was abandoned in the 4th century AD [64]. The whale bone analysed in the present study (WH810) was recovered in 1996 from the inside of a house, at a pre-Roman stratigraphic level dated to the 4th or 3rd centuries BC [32].

Collagen PMF and Ancient DNA Barcoding

Collagen PMF (ZooMS)

A sample of between 10-30 mg of bone powder was fully demineralized through immersion in 0.6 M hydrochloric acid at 4°C. Each samples was then centrifuged, the supernatant was discarded, and then rinsed three times with 200 µl of 50 mMol ammonium bicarbonate, pH 8.0 (AmBic solution), before being gelatinised in 100 µl of AmBic solution at 65°C for 1 hour. The gelatinised collagen was incubated with 0.4µg of trypsin at 37°C overnight, then subsequently acidified to 0.1% trifluoroacetic acid (TFA). The collagen was purified using a 100 µl C18 resin ZipTip® pipette tip (EMD Millipore) with conditioning and eluting solutions composed of 50% acetonitrile and 0.1% TFA and washing solution composed of 0.1% TFA; the samples were eluted in a volume of 50 µl. Equal amounts of the collagen extract and α-cyano-hydroxycinnamic acid matrix solution (1% in conditioning solution) were mixed (1 µl each) and spotted onto a 384 spot MALDI target plate, with calibration standards. Samples were spotted in triplicate, and run on a Bruker ultraflex III MALDI TOF/TOF mass spectrometer with a Nd:YAG smart beam laser. A SNAP averaging algorithm was used to obtain monoisotopic masses (C 4.9384, N 1.3577, O 1.4773, S 0.0417, H 7.7583), resulting in a total of 36 individual spectra, which have been uploaded to the Dryad Digital Repository [65].

We used the mMass software [66] to visually inspect the spectra; spectra from replicates of the same sample were averaged, and compared to the list of *m/z* markers for marine mammals presented in [67–69]. Taxonomic identifications were assigned at the most conservative level of identification (genus, or family level) based on the presence of unambiguous *m/z* markers (table S4).

Table S4 Designated collagen peptide markers used for taxonomic identification of the archaeological bone samples. “?” indicates peak is present but at low intensity, or below signal to noise threshold.

Sample	(P1)	α2(I)988– 1000(A)	α2(I)494– 508(B)	α2(I)512– 529(C)	(P2)	α2(I)803– 826(D)	α1(I)602– 634(F)	α2(I)767– 799(G)	ZooMS ID
WH810	1079	-	1453	1566	1652	2135	2899	3023	Gray whale
WH812	1079	-	1453	1577	1682	2135	2883	-	Balaenidae
WH813	1079	-	1453	1566	1652	2135	-	-	Fin/Humpback/Gray whale
WH814	1063	-	1453	1566	1638	2119	2883	3023	Risso's dolphin/Pilot whale/ False killer whale
WH815	1079	1205	1453	1566	1652	2135	2899	3023	Gray whale
WH816	1079	-	1453	-	-	2119	2883?	-	Dolphin/Porpoise/ Orca
WH817	1079	1205	1453	1550	1652	2133	2883	3039	Sperm whale
WH818	1079	1205	1453	1577	1682	2135	2883	3023	Balaenidae
WH819	1105	-	1453	1579	-	2115	2853	3015?	Elephantidae
WH820	1079	1205?	1453	1566	1652	2135	2899	3023	Gray whale
WH821	1079	1205?	1453	1566	1652	2135	2899	3023	Gray whale
WH822	1079	1205	1453	1577	1682	2135	2883	3023	Balaenidae

DNA Barcoding

DNA from the archaeological whale bones was extracted in the dedicated Ancient DNA laboratory at University of York, which follows strict protocols for contamination control and detection, including positive pressure, the use of protective clothing, UV sources for workspace decontamination, laminar flow hoods for

extraction and PCR-set-up, and separation of pre- and post-PCR workspaces and related equipment and consumables. Bone fragments were decontaminated through immersion in 6% sodium hypochlorite for 5 mins, rinsed two times in HPLC grade water, UV irradiated for 30 min on two sides, before being ground into powder. DNA was extracted using a silica spin column protocol ([70], as modified in [71]); the purified DNA was eluted in 50ul. Initial PCR amplifications targeted a 182bp fragment of the mitochondrial cytochrome b gene which has been demonstrated to successfully distinguish cetacean species [72,73] using PCR reactions and cycling conditions followed those described in [74]. Those samples that has been initially identified as cetacean species using collagen PMF, but which failed initial PCR amplifications were re-amplified with primer sets designed to target the same cytochrome b region, using an overlapping primer sets with amplicons of <100 bp (table S5). For samples where the collagen PMF identification pointed to Elephantidae, cytochrome b primer sets were deigned to target 116 bp and 167 bp fragments from extinct and extant species within the genera *Loxodonta* and *Elephas* (table S5). No successfully sequenced products were retrieved using either of the Elephantidae primer sets. Successfully amplified products were sequenced using the forward and/or reverse primers at Eurofins Genomics, Ebersberg, Germany.

ChromasPro software (www.technelysium.com.au) was used to visually analyse and edit the sequences and truncate primer sequences. Sequences were compared with published references through the GenBank BLAST application (<http://www.ncbi.nlm.nih.gov/BLAST/>), with multiple alignments of ancient and published reference was sequences conducted using ClustalW [75], through BioEdit (<http://www.mbio.ncsu.edu/BioEdit>). Species identifications were assigned to a sample only if it was identical to published reference sequences from a single species in GenBank; cetacean species identities were further confirmed through ‘DNA Surveillance’, a web-based programme which provides robust cetacean identifications based on comparisons with a comprehensive set of validated cetacean reference sequences [76]. Seven samples produced unambiguous species identifications to the species level; WH816 could only be assigned to the genus *Delphinus*, with identical matches to long-beaked common dolphin (*Delphinus capensis*) and short-beaked common dolphin (*Delphinus delphis*). Eight sequences were uploaded to the Genetic Sequence Database at the National Center for Biotechnical Information (NCBI) (GenBank ID: MH193488-95).

Table S5. Cytochrome *b* primer sets used to amplify the archaeological bone samples. WH indicate cetacean primers, F indicated forward primer, R indicates reverse primer. Coordinates for whale primers based on the *Eschrichtius robustus* mitogenome (Genbank accession NC005270); coordinates for the elephant primers are based on the *Loxodonta africana* mitogenome (Genbank Accession NC000934). Primers WH-F1 and WHR182 from [72].

Primer	Sequence (5' to 3')	Coordinates	Amplicon
WH-F1	ATGACCAACATCCGAAAAACAC	14201-14222	182 bp
WH-R182	GTTGTTGTGTCTGGTGTGTAGTGTATT	14356-14382	
WH-R87	ATGATGRAACTTCGGCTCYCTACT	14287-14310	87 bp (with WH-F1)
WH-F109	AGGGAGCCGAAGTTYCATCAT	14287-14307	95 bp (with WH-R182)
EL-F93	AAATTTCCGGCTCACTACTAGGAG	14239-14261	116 bp
EL-R209	CAGATATGGGRTATRGATGAAAATGC	14330-14355	
EL-R260	GCTCCGTTGAGTGYAGTTGTCG	14384-14406	167 bp

Dating

Stratigraphical dating

The stratigraphical dating method [77] is based on the combination of a relative dating of samples from the position of the layer where they are found in relation to the position of other layers (more ancient/more modern); and an absolute dating based on the archaeological finds found inside the layers, such as pottery, glass, and coins. In Historic archaeology, stratigraphical dating is generally enough and considered much more accurate than the radiocarbon dating or other absolute chronology methods, that are applied where no artefact information is available or to earlier periods (Prehistory, earlier phases of Protohistory), where the dating range of artefacts is not so precise.

Most specimens analysed in this study come from recent archaeological excavations by well-trained university research teams and local administration archaeology units, and for these dating was possible through the stratigraphical method (table 1; see references in table S3 for details). Three of the specimens come from more ancient excavations. Specimen WH810 was found inside a pre-Roman house, at a stratigraphic level dated to the 4th or 3rd centuries BC [32]; in the case of WH812, no contextual or chronological evidence was available; in the case of WH822, an approximate dating was inferred from field records from the excavation that indicated the position of the sample in the archaeological site and associated artefacts (north African imported pottery and coins).

Radiocarbon dating

Radiocarbon dating is a technique used for determining the age of organic materials, by measuring the amount of radiocarbon (^{14}C , a radioactive isotope of carbon) that is present in the material in relation to that in the atmosphere, given known rates of radioactive decay. Radiocarbon present in the atmosphere combines with oxygen to form radioactive carbon dioxide, which is incorporated into plant tissues via photosynthesis, and then into animal tissues via consumption. When the plant/animal dies, it stops exchanging carbon with its environment, and the amount of ^{14}C declines via radioactive decay, whereas the amount of the non-radioactive ^{12}C isotope remains broadly constant. Hence, a lower ratio of ^{14}C in relation to ^{12}C corresponds in general to an older the specimen. However, converting ^{14}C concentrations to calendar years requires calibration by an appropriate curve obtained from absolutely dated chronologies (e.g., from tree-rings, corals) [78]. In particular, dating of marine animals needs to take into account the so-called marine reservoir effect: as oceans are depleted in ^{14}C in relation to the atmosphere, conventional radiocarbon dates for marine organisms appear older than for contemporary terrestrial individuals [79]. The dataset currently recommended for calibrating radiocarbon dates of marine samples is the Marine13 calibration curve [78]. Accordingly, we calibrated all our records using this dataset (Table S3), using the radiocarbon calibration programme Calib 7.1.0 (<http://calib.org/calib/calib.html>) [80].

Dating of marine specimens can further be refined by taking into account the fact that the marine reservoir effect varies across oceanic (polar waters having larger reservoir ages than equatorial ones) [79]. In the case of the North Atlantic and gray whales, the relevant water masses for estimating the marine reservoir effect are those of their (high latitude) feeding grounds (figure 1), rather than the oceans adjacent to the coasts where the bones were found (which are likely calving, non-feeding, areas). Mangerud and colleagues [81] measured directly the marine reservoir effect in a North Atlantic whale individual captured in Iceland in 1891, estimating a value of 425 years. The marine reservoir effect may be different for Gray whales (which feed at higher latitudes and have a different diet) and for the other species in our analyses (which probably fed at lower-latitude waters). In the absence of more detailed information, we did not correct for the spatial

variation in marine reservoir effect (i.e., we used a deltaR correction value of 0+/-0 in the calibration with Marine13).

Interpretation of dating results

The two dating methods do not measure the same thing: radiocarbon indicates the date at which the whale was alive (and still growing); the stratigraphical dating corresponds to the date when the bone material was last abandoned (potentially long after the whale died). It is thus expected that the former is older than the later, with the date of most interest to this study – when the animal died – somewhere in between. For the two specimens of gray whale (WH815, WH820/21), the two of right whale (WH818, WH822) and the one of sperm whale (WH817) for which we had results from the two dating methods, the results were in the expected direction: the radiocarbon dating (corrected for the marine reservoir) was older than the stratigraphical dating (table 1). However, for the specimens of pilot whale (WH814) and of dolphin (WH816) the opposite happened, such that the relationship between the dates obtained via radiocarbon dating and via stratigraphical methods is nonsensical. These inversions can be explained by variations in the local marine reservoir effect (a negative deltaR value) and/or problems in the stratigraphic sequence (for example, caused by post-depositional modification of the deposit). It is beyond the scope of this study to analyse the relative merits and uncertainties of these two dating methods. Furthermore, it is not crucial in this study to obtain exact dates. What is most relevant to our conclusions is that both methods provide evidence that right and gray whales occurred in the Strait of Gibraltar region during the Roman period.

Appendix 3. Historical accounts mentioned in the main text

Killer whales attacking whale cows and calves - Pliny the Elder, Naturalis Historia

Pliny's "Natural History" is an encyclopaedic work covering all aspects of the natural world (from astronomy to geology to zoology), published in the first century AD, originally in Latin. The text here (book 9.5) was translated by Bostock & Riley [82].

"The balæna penetrates to our seas even. It is said that they are not to be seen in the ocean of Gades before the winter solstice, and that at periodical seasons they retire and conceal themselves in some calm capacious bay, in which they take a delight in bringing forth. This fact, however, is known to the orca, an animal which is peculiarly hostile to the balæna, and the form of which cannot be in any way adequately described, but as an enormous mass of flesh armed with teeth. This animal attacks the balæna in its places of retirement, and with its teeth tears its young, or else attacks the females which have just brought forth, and, indeed, while they are still pregnant: and as they rush upon them, it pierces them just as though they had been attacked by the beak of a Liburnian galley. The female balænæ, devoid of all flexibility, without energy to defend themselves, and over-burdened by their own weight, weakened, too, by gestation, or else the pains of recent parturition, are well aware that their only resource is to take to flight in the open sea and to range over the whole face of the ocean; while the orcæ, on the other hand, do all in their power to meet them in their flight, throw themselves in their way, and kill them either cooped up in a narrow passage, or else drive them on a shoal, or dash them to pieces against the rocks. When these battles are witnessed, it appears just as though the sea were infuriate against itself; not a breath of wind is there to be felt in the bay, and yet the waves by their pantings and their repeated blows are heaved aloft in a way which no whirlwind could effect."

Interpretation

This description could very feasibly apply to either right whales or gray whales (as well as humpback whales) being attacked in their calving grounds by killer whales (orcas). If so, this is a very ecologically accurate description. In particular:

- The appearance of the pregnant whales around the winter solstice – both gray whales and right whales calve during the winter, typically arriving by the end of December, with most births occurring between late December and March, with a peak in January [22,83].
- Whales "bringing forth" in a calm and capacious bay – gray whales calve in lagoons [22], right whales in sheltered coastal areas [83].
- Orcas as "*peculiarly hostile to the balæna*" – some ecotypes of killer whales specialise on marine mammal prey, being the main predators of large baleen whales, particularly of their calves [84].
- Orcas attacking calves and cows in their calving areas – most recorded attacks of right and gray whales by killer whales calves are in the calving grounds [84]. Calves are the main targets, but as cows actively defend and protect the young, and killer whales attempt to separate the two [84], to an external observer it may easily appear as though the orcas are attacking the females too.
- Pliny describes orcas attempting to corner the whales against the shoreline, and the whales attempt to escape into the open ocean. In reality, the opposite happens: when attacked by killer whales, right and gray whales move closer to the coast as a form of protection [84]. However, to an external observer it may appear as though the orcas have cornered the whales against the shore.
- Much sea agitation as a result of these attacks ("as though the sea were infuriate against itself") – right whales and gray whales actively defend themselves and their calves from killer whales by rolling and trashing their tail flukes, producing substantial splashing [84].

“Ram-fishes” spending the winter between Corsica and Sardinia - Aelian, De Natura Animalium

Aelian’s “On the Nature of Animals”, is a collection of brief stories of natural history, published ca. 200 AD, originally in Greek. Text presented here (from book 15:2) is the translation by Scholfield [85].

“Ram-fishes, whose name has a wide circulation, although information about them is not very definite except in so far as displayed in works of art, spend the winter near the strait between Corsica and Sardinia and actually appear above water. And round about them swim dolphins of very great size. Now the male Ram-fish has a white band running round its forehead (you might describe it as the tiara of a Lysimachus or an Antigonus or of some other king of Macedon), but the female has curls, just as cocks have wattles, attached below its neck. Male and female alike pounce upon dead bodies and feed on them, indeed they even seize living men, and with the wave caused by their swimming, since they are large and of immense bulk, they even overturn vessels, such a storm do they unaided raise against them. And they even snatch men standing on the shore close at hand. The inhabitants of Corsica tell how, when a ship was wrecked in a storm, a man who was a very strong swimmer managed to swim over a wide expanse of sea and to secure a hold on some headland in their country; he climbed out and stood there, all fear banished, for he was now free from all perils, with no anxiety for his life, his own master. Now a Ram-fish which was swimming by caught sight of him as he stood, and inflamed with hunger turned about, arched its back, and with its tail drove a great mass of water forward, and then rose as the swelling wave lifted it, and in a moment was carried up on to the headland and like a hurricane or whirlwind seized the man. So much for the Ram-fish's prey ravished off Corsica.

Those who live on the shores of Ocean tell a fable of how the ancient kings of Atlantis, sprung from the seed of Poseidon, wore upon their head the bands, from the male Ram-fish, as an emblem of their authority, while their wives, the queens, wore the curls of the females as a proof of theirs. Now this creature has exceedingly powerful nostrils and inhales a great quantity of breath, drawing to itself an immense amount of air; and it hunts seals in the following manner. Directly the seals realise that a Ram-fish is somewhere close at hand, bringing destruction upon them, they swim ashore with all possible speed and pass over the land and plunge into the shelter of rocky caverns. But the Ram-fish perceive that they have fled and give chase, and as they face the cave they know from the smell of flesh that their prey is within, and, as though by some all-powerful spell, with their nostrils they draw in the air that intervenes between themselves and the seal. But the seal avoids the attack of the monster's breath, as it might an arrow or a spear-point, and at first withdraws, but is finally dragged out of the cave by the overmastering pull and follows, against its will, just as though it were bound fast with thongs or cords, and shrieking provides the Ram-fish with a meal.

Those who are skilled at exploring these matters assert that the hairs which grow from the nostrils of the Ram-fish serve many purposes.”

Interpretation

The description of “ram-fishes” (*Kpīoc*, *aries*) as predators of both seals and men has led previous authors to assume they correspond to killer whales [85,86]. Killer whales are indeed predators of seals (not of humans), and even if the method described for preying on seals (attracted from their caves by the whale’s breath) has little correspondence with reality, the method described for snatching humans from the shore (“with the wave caused by their swimming”) is curiously reminiscent of the method killer whales in the Antarctica use to dislodge Weddell seals from ice floes [87]. Pliny also mentions “rams” in his *Naturalis Historia* (placing them in the Atlantic coast of France), describing them as having “only a white spot to represent horns” [NH, 9:4], leaving subsequent authors to presume this described the white spot above the eye in killer whales [82].

However, there are multiple details in Aelian's description that are not compatible with ram-fishes being killer whales, but which match right whales (and possibly humpback whales). Aelian describes two types of ram-fish: the male with "*a white band running round its forehead (you might describe it as the tiara of a Lysimachus or an Antigonus or of some other king of Macedon)*", and the female with "*curls, just as cocks have wattles, attached below its neck*". The white band like a tiara is not easily reconcilable with the killer whale's white spot, and the curls like wattles even less so. Following from a previous work [8] we argue that these could correspond, respectively, to the head callosities of right whales (figure S4) and the deep ventral grooves of humpbacks whales (figure S5). The callosities of right whales make strong white patterns in the head (in contrast with dark skin) that are compatible with Aelian's description of "*a white band running round its forehead*", like a "*tiara*". Furthermore, their appearance (calcified patches of skin, often encrusted with barnacles) can feasibly be seen to "*represent horns*" (as noted by Pliny), which could also explain the name "ram-fish" (*aries*). Gray whales have ventral grooves too, but they are not nearly as remarkable as those of humpbacks, and seems unlikely that they would have been described as "wattles", so we find it unlikely that female ram-fishes could correspond to gray whales.

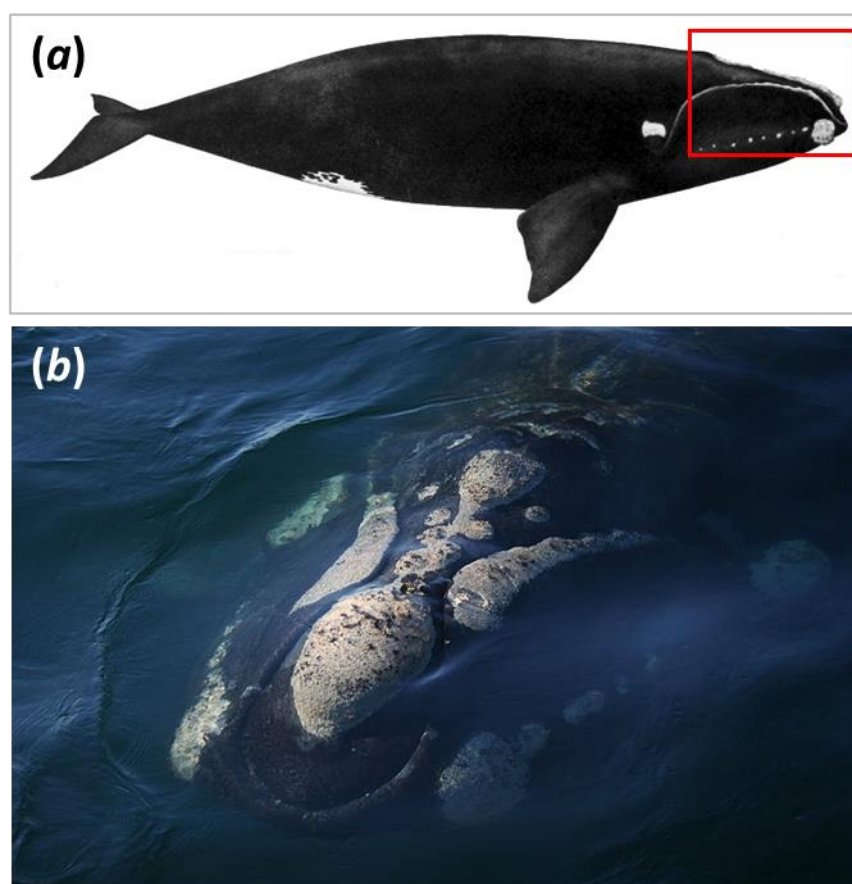


Figure S4. Right whale head callosities: (a) location (illustration from NOAA NOAA United Statesm, National Marine Fisheries Service; public domain); (b) close-up of the whale's rostrum, showing the "bonnet", the largest callosity (here, a southern right whale, *Eubalaena australis*; Photo by Michaël Catanzariti, public domain).

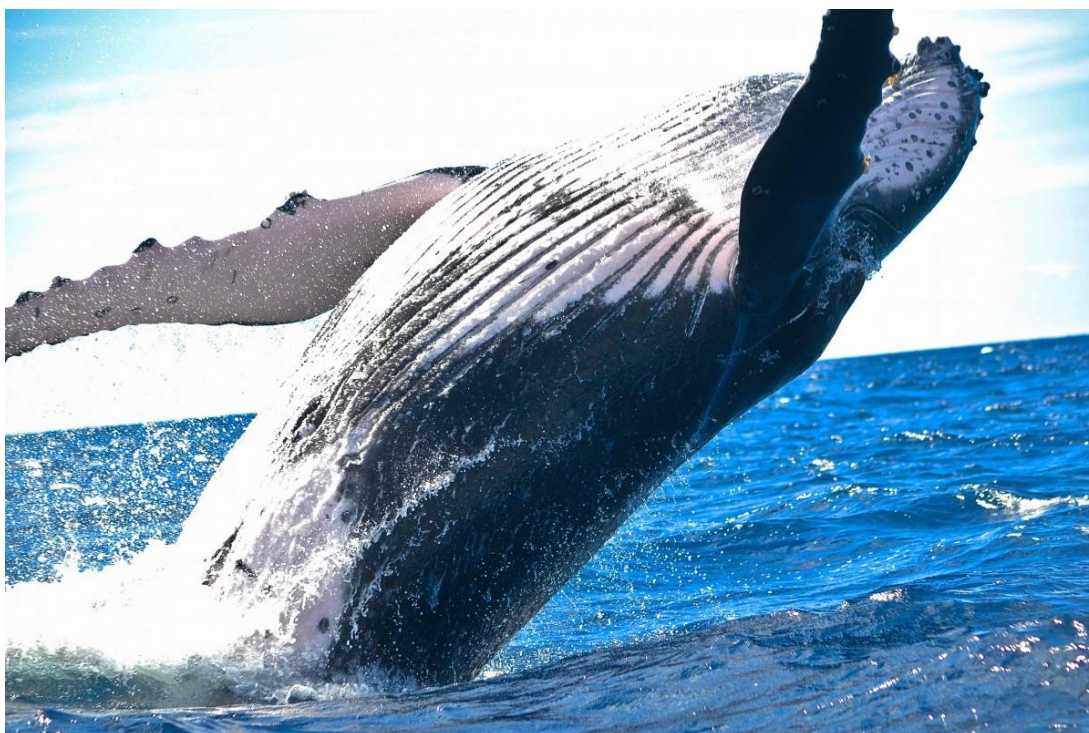


Figure S5. Humpback whale breaching, showing the ventral grooves (photo by unknown photographer, public domain; <https://pxhere.com/en/photo/63183>).

Another detail pointing in the direction of baleen whales in general, and right whales in particular, is the reference to “*hairs which grow from the nostrils*” and which “*serve many purposes*”. These could correspond to baleen, which in right whales are particularly long and flexible, and were historically a very valuable material [88].

Right whales (and humpback whales) could feasibly “*spend the winter near the strait between Corsica and Sardinia*” if this was a calving ground, whereas it is not straightforward to find a hypothesis for explaining the same seasonal pattern for killer whales.

Aelian also notes that ram-fishes “*actually appear above water*”, which could correspond to breaching behaviour (i.e., jumping clear of the water), that right whales, humpback whales and killer whales all exhibit (e.g., figure S5). Finally, his description that “*round about them swim dolphins of very great size*” could potentially refer to calves.

Sea-monster hunting scene - Oppian, Haliaeutica

Oppian’s *Haliaeutica* is a long poem about fishing, originally in Greek, written in the late 2nd or early 3rd centuries, probably in Malta [86]. Among other species of “fish”, it mentions sea-monsters (plural Κήτεα, singular κήτος = cetus), including an epic hunting scene that has frequently been assumed to correspond to a whaling scene [86]. However, Oppian (like others in this period [89]) uses the term Κήτεα in a broad sense to mean “large marine animal”, including not only whales, but also dolphins, sharks, tuna, seals and turtles. Here we briefly discuss Oppian’s cetus-hunting scene in the context of species’ ecology and historical whaling methods, using the translation by Mair [86].

The scene described (*Haliaeutica* 5:75-380) is a highly coastal activity: the beasts “*stray and come nigh the beach where the water is deep inshore: and there one may attack them*”. Hunting starts with the beast

apparently stranded (*"Many a time in his wandering he runs aground on rock or beach [...] Thereupon with eager thoughts the fishers hasten to the labour of the hunt"*) but the subsequent description indicates an animal that can escape (*"dives swiftly into the nether gulfs of the sea"*), suggesting overall that the animal is targeted very close to shore, perhaps in low-depth areas. The activity is so close to shore that, once the beast is hooked, *"one of the whalers row his hollow skiff and come to land and make fast the line to a rock upon the shore"* and the entire scene is visible to a potential observer who *"standing on a cliff beholds the tremendous toil of the men in this warfare of the sea"*.

The method described is a collective hunting activity, with many points in common with coastal whaling methods used elsewhere. In particular: hunters approach the beast quietly in rowing boats (*"well-benched ships"*, *"with quiet oars they gently make white the sea, carefully avoiding any noise, lest the great κῆτος remark aught and dive into the depths for refuge"*); they attack the beast using a harpoon system consisting of a hook connected to a long cord, such that when the beast is first hooked and *"in the anguish of fiery pain he dives swiftly into the nether gulfs of the sea"*, *"speedily the fishers allow him all the length of the line [...] for easily could he drag them to the bottom, benched ship and all together"*. All of these methods are reminiscent of Basque whaling [90]. Furthermore, the fishers use floaters – *"large skins, filled with human breath and fastened to the line"* that hinder the escape of the beast and signal its presence, similarly to autochthonous whaling methods from the Pacific and Arctic Oceans (e.g., by the Makah Indians of North America [91]).

However, two characteristics of this hunting point away from whales. First, the hunters use bait (*"for fatal banquet, they put upon the hook a portion of the black liver of a bull or a bull's shoulder suited to the jaws of the banqueter"*; *"from the prow they launch for the giant beast the fatal snare"*) that the beast cannot resist (*"And when he [the beast] espies the grievous banquet, et springs and disregards it not obedient to his shameless belly, and rushing upon the hooked death he seizes it"*). Second, once the beast is dead and on the shore, *"some marvel at the deadly ranks of his jaws, even the dead and stubborn tusks, like javelins, arrayed in triple row with close-set points"*. The multiple rows of pointy teeth are characteristic of sharks.

Mair [86] proposes that the hunted beast could be a sperm whale, the only large whale with teeth; but that does not address the issue of the bait, or of the triple row of pointy teeth. On the other hand, big sharks as well as sperm whales are not animals that one would typically expect to capture near the coast. In our opinion, Oppian's κῆτος-hunting scene likely contains a mix of details from multiple methods for fishing large marine animals, possibly including whales. As such, we present it here not so much as evidence of whaling in the Roman period, but to illustrate that sophisticated cooperative fishing methods similar to those used by coastal whalers elsewhere were in place at the time.

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